

The Maintenance of Polymorphism and Cryptic Mimesis in the Limpet *Scurria variabilis* by Two Species of *Cinclodes* (Aves: Furnariinae) in Central Chile

by

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Abstract. On the central Chilean coast, the intertidal limpet *Scurria variabilis* is clinally polymorphic, ranging from essentially non-cryptic individuals to individuals that are highly cryptically mimetic with a barnacle model. Many species prey on *S. variabilis*, but birds, notably waders, such as oystercatchers, and two species of *Cinclodes* are the only visual, selective predators present. The influence of *Cinclodes* on limpet polymorphism is evidenced by the predominance of cryptic morphs in habitats accessible to *Cinclodes*. Such differences in morph ratios between accessible and inaccessible habitats were not present in areas without avian predators or where shorebirds, but not *Cinclodes*, were present. There is no evidence of genetic influence by avian predators on local *Scurria* populations, although survival of individual *Scurria* limpets is favored by polymorphism and particularly by cryptic mimesis. Selective predation is considered to be the mechanism maintaining the polymorphism, but under present conditions of predation, polymorphism is not considered necessary for survival of the *Scurria* population as a whole.

INTRODUCTION

Eucrypsis by virtue of homochromy and, to some extent, active selection of specific substrata have been demonstrated to increase survival of *Collisella* limpets (Mollusca: Patellidae) in Pacific North America (GIESEL, 1970; MERCURIO *et al.*, 1985). Until recently the distribution of the genus *Collisella* was thought to extend to Chile in Pacific South America, with the limpet community of the mid-littoral of the Chilean coast being dominated by one species, *C. araucana* (d'Orbigny, 1839) (MARINOVICH, 1973; CASTILLA, 1976). The taxonomy of South American patellaceans is poorly understood. Examination of specimens of "*C. araucana*" collected in central Chile in November 1985 shows that, on the basis of shell-structure characters and plumbing of the heart vessels, these specimens belong to the genus *Scurria* and are probably *S. variabilis* (Sowerby, 1839) (D. R. Lindberg, *in litt.*). The mid-littoral of central Chile is characterized by extensive beds of small barnacles, principally *Chthamalus cirratus* Darwin (CASTILLA, 1981), and *S. variabilis* occurs both on bare rock surfaces and among these barnacle beds. *Scurria variabilis* is clinally polymorphic, ranging from individuals that are essentially non-cryptic to individuals exhibiting extraordinary cryptic

mimesis (*sensu* PASTEUR, 1982) due to homomorphy and homochromy with the model *C. cirratus* (Figure 1). BOEHME (1974) erroneously described the barnacle-like morph of *S. variabilis* as a new species, *Collisella boehmita*.

Polymorphism in certain marine species has been shown to be adaptive in reducing predator hunting success (*e.g.*, HOAGLAND, 1977; REIMCHEN, 1979; PALMER, 1985). In such instances it is reasonable to conclude that predation pressure is a prime selective force in the evolution of polymorphism or mimicry in the prey species, although the process by which a relative advantage accrues to divergent phenotypes in the early stages of divergence has been demonstrated on few occasions (BROWER *et al.*, 1971). Mimicry in *Scurria variabilis* is visual and for any selective advantage to accrue to mimetic individuals the predator(s) of *S. variabilis* must be assumed to forage both visually and selectively. Intertidal predators in central Chile are numerous and diverse, and many species have been studied in detail (PAINE & PALMER, 1978; CASTILLA, 1981; BAHAMONDES & CASTILLA, *in press*). The only predators present that forage selectively using visual cues and prey on *S. variabilis* are certain shorebirds (Aves: Charadriiformes) and two species of *Cinclodes* (Aves: Furnariinae) (CASTILLA, 1981;

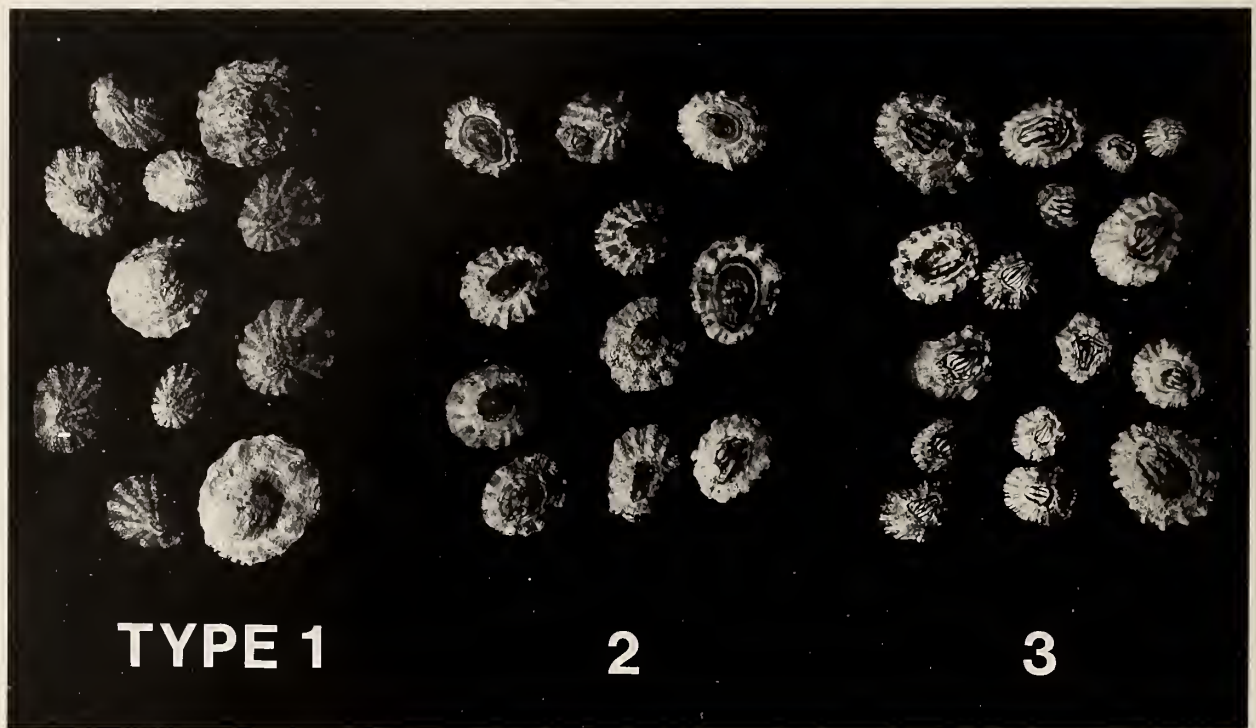


Figure 1

The three recognized morphs of *Scurria variabilis*. Type 1 = non-cryptic; Type 2 = intermediate; Type 3 = cryptically mimetic.

BAHAMONDES & CASTILLA, in press, and personal observations). This study quantifies the occurrence of polymorphism and mimicry in *S. variabilis* and identifies the predators most likely to be responsible for maintaining that polymorphism, based on predator occurrence and foraging behavior and on variations in morph ratios of *S. variabilis*.

MATERIALS AND METHODS

Three morphs of *Scurria variabilis* were recognized: Type 1 exhibited no cryptic coloration or modification of shape; Type 2 had a well-defined darker area apically, corresponding approximately to the area occupied by the tergal and scutal plates of a sessile barnacle; and, Type 3 was cryptically mimetic, being in all respects, including the outline of the tergum and scutum, an excellent mimic of *Chthamalus* (Figure 1). The mimicry of Type 3 limpets was so precise that on occasions it was necessary to remove the animal from the rocks to determine whether it was a limpet or a barnacle.

Absolute and relative frequencies of occurrence of the three morphs were recorded at 17 sites in central Chile between 30°S and 42°S during October and November 1985 (Figure 2). At each site, frequencies of occurrence of the three *Scurria* morphs were recorded in the mid-littoral using randomly positioned 10 × 10 cm quadrats

in two habitat types: (1) rocky slopes or flat areas accessible to avian predators and (2) vertical or steep rock faces inaccessible to avian predators. Between 8 and 76 quadrats (0.08–0.76 m²) were sampled, dependent on limpet density. Limpet densities per m² were calculated by simple extrapolation from the area sampled at each site. Hence, confidence limits are not presented.

The number of intertidal avian predators present per 100 m of shore at each site was assessed, and on this basis three types of site were recognized: sites without avian predators, sites with *Cinclodes* but with no (or very few) shorebirds, and sites with many shorebirds but no *Cinclodes*.

RESULTS

At 13 of the 17 sites, less than 1% of all *Scurria variabilis* were >12 mm in length (12 mm corresponding to the size of a large specimen of *Chthamalus cirratus*). At sites Algarrobo 2 and 3, and at Ancud 1 and 2, up to 85% of all *S. variabilis* were >12 mm in length.

At sites without avian predators there were (with one exception) no significant within-site differences in the ratios of the three *Scurria* morphs on rock faces accessible and inaccessible to birds, but there was no consistency in morph ratios among sites (Table 1). In addition, there were no significant differences in the proportions of crypti-

cally mimetic (Type 3) morphs in the four habitats where birds had no direct predatory impact *viz.*: accessible and inaccessible habitats at sites without avian predators, and inaccessible habitats at sites where either waders or *Cinclodes* were present (Kruskal-Wallis one-way ANOVA, $N_1 = 4$, $N_2 = 4$, $N_3 = 4$, $N_4 = 9$, $H = 5.51$, $P = 0.138$).

At eight of the nine sites with *Cinclodes* present, there was a significant difference in morph ratios between accessible and inaccessible rock faces. Non-cryptic (Type 1) morphs formed a higher proportion of the *Scurria* population on inaccessible than on accessible rock faces (mean = $35.2 \pm$ SD of 21.7% vs. $17.3 \pm 16.2\%$) (Wilcoxon matched-pairs signed-rank test, $n = 9$, $T = 0.00$, $P = 0.008$) and the reverse was true of Type 3 morphs ($38.1 \pm 16.9\%$ vs. $52.9 \pm 19.4\%$; $n = 9$, $T = 1.00$, $P = 0.011$). Type 2 morphs were slightly better represented in accessible ($\bar{x} = 29.8 \pm 14.3\%$) than in inaccessible ($\bar{x} = 26.7 \pm 12.5\%$) habitats, but the difference was not significant ($n = 9$, $T = 9.00$, $P = 0.110$). In addition, the site with the highest density of *Cinclodes* (*viz.* Los Molles 1) showed the greatest difference between morph ratios in accessible and inaccessible sites, with the limpet population on accessible rocks being strongly biased towards mimetic individuals (Table 1, Figure 3).

Densities of foraging shorebirds were much higher than those of *Cinclodes* (up to 200 birds per 100 m of shore) but, at sites where shorebirds were present, the proportions of non-cryptic (Type 1) and mimetic (Type 3) *Scurria* in accessible and inaccessible habitats were not significantly different (Wilcoxon matched-pairs signed-rank test: Type 1, $n = 4$, $T = 0.00$, $P = 0.068$; Type 3, $n = 4$, $T = 3.00$, $P = 0.465$).

DISCUSSION

True mimicry in limpets is rare. There is a morph of the Pacific *Collisella stanfordiana* that resembles the toxic onchidiid *Hoffmanola hansii* (YENSEN, 1973), an example of Batesian mimicry. There is a barnacle-imitating morph of the Australian *Patelloida latistrigata* (G. M. Branch, personal communication) and in the Gulf of California, *Collisella acutapex* resembles the barnacle *Balanus amphitrite* (YENSEN, 1973). The adaptive advantage of these mimics has not been investigated. *Scurria variabilis* exhibits clinal polymorphism, with an extreme morph showing cryptic mimicry of *Chthamalus* barnacles.

On the central Chilean coast there are several vertebrate and invertebrate predators of limpets (reviewed by CASTILLA, 1981), but most of these have been shown to remove both limpets and barnacles using tactile stimuli in a non-selective manner. Examples of such predators are the sea-star *Heliaster helianthus* (Lamarck, 1816), the muricid *Concholepas concholepas* (Bruguière, 1789) (CASTILLA *et al.*, 1979; CASTILLA, 1981) and the suckerfish *Sicyopterus sanguineus* Muller & Troschel (PAINE & PALMER, 1978; CASTILLA, 1981). Small numbers of *Scurria variabilis* have been found in the gut of the surfbird *Aphriza virgata* (Gmelin, 1789), possibly ingested coincidentally when feeding



Figure 2

Map of the study area.

on its preferred prey, the mussel *Semimytilus algosus* (R. Navarro, personal communication). The Kelp Gull *Larus dominicanus* preys on intertidal limpets, but *Scurria variabilis* is not an important prey species, the larger eulittoral

Table 1

Morph ratios and densities of *Scurria variabilis*, and densities of *Cinclodes* spp. at 17 sites in central Chile, October–November 1985.

Site type Study site	<i>Scurria</i> density/m ²		<i>Cin- clodes</i> density/ 100 m	Sp.†	Accessible habitat Morph type (%)				Inaccessible habitat Morph type (%)				χ^2	P
	Acc.	Inacc.*			1	2	3	N	1	2	3	N		
No avian predators														
Totalillo 1	183	263	0.0		31	15	54	139	40	11	49	137	2.72	n.s.
Los Molles 3	684	804	0.0		69	15	16	171	57	17	26	201	-7.84‡	<0.05‡
Los Molles 4	1141	1100	0.0		19	21	60	194	16	13	71	176	4.98	n.s.
Los Molles 5	950	3725	0.0		19	32	49	190	16	41	43	298	3.03	n.s.
+ <i>Cinclodes</i>														
Totalillo 2	635	460	1.0	ni	1	40	59	165	15	30	55	138	18.85	<0.001
Los Molles 1	2770	418	6.0	ni	2	19	79	277	33	18	49	117	85.21	<0.001
Los Molles 2	low	low	1.3	ni	43	7	50	129	76	3	21	90	23.58	<0.001
Algarrobo 1	628	757	0.2	ni	38	21	41	113	62	16	22	106	12.36	<0.01
Punta El Lacho	2153	1205	1.0	ni	28	52	20	323	37	42	21	241	8.01	<0.05
Mehuín 1	464	374	1.0	pa	6	28	66	116	19	31	50	131	8.77	<0.05
Mehuín 2	760	527	0.6	pa	1	22	77	152	9	26	65	158	11.53	<0.01
Ancud 1	244	179	1.0	pa	19	33	48	122	31	34	35	125	5.93	n.s.
Ancud 2	543	271	1.0	pa	18	46	36	190	35	40	25	95	9.47	<0.01
+ Shorebirds														
Algarrobo 2	318	79	0.0		45	33	22	159	69	17	14	35	6.99	<0.01
Algarrobo 3	952	low	0.0		45	41	14	238	64	17	19	47	9.70	<0.01
Las Salinas 1	703	610	0.0		40	29	31	207	45	34	21	183	4.35	n.s.
Las Salinas 2	1133	893	0.0		35	43	22	345	46	26	28	268	18.28	<0.001

* Acc. = Accessible, Inacc. = Inaccessible.

† ni = *Cinclodes nigrofumosus*, pa = *Cinclodes patagonicus*.

‡ At this site there were more cryptic limpets on inaccessible slopes, an opposite trend to that found elsewhere. This is indicated by a negative χ^2 value.

Collisella zebrina being taken preferentially (BAHAMONDES & CASTILLA, in press). The marine otter *Lutra felina* (Molina, 1782) occurs commonly on exposed coasts in central Chile, but its intertidal feeding activity is confined to the eulittoral zone and *Scurria variabilis* is not recorded as a prey item (CASTILLA & BAHAMONDES, 1979). The extent of predation by fish other than *Sicyaces sanguineus* during the high tide period is unknown, but few, if any, species other than *Sicyaces sanguineus* are likely to possess the morphological adaptations necessary to remove limpets from rock faces.

Based on the above, we hypothesized that the predators most likely to be morph-specific in their predation of *Scurria variabilis* were the Blackish Oystercatcher, *Haematopus ater* Vieillot & Ondart, 1825, which is recorded as preying on *S. variabilis* (CASTILLA, 1981), and two species of *Cinclodes*, an avian genus endemic to South America (HOWARD & MOORE, 1980). The Seaside *Cinclodes* *C. nigrofumosus* (d'Orbigny & Lafresnaye, 1838) and the Duskybellied *Cinclodes* *C. patagonicus* (Lesson, 1828) both occur on the coast of central Chile, although the former does not occur south of about 39°S (JOHNSON & GOODALL, 1967). *Cinclodes nigrofumosus* is exclusively coastal, whereas *C. patagonicus* occupies a range of habitats: both species include

mid-intertidal barnacle beds within their range of foraging habitats and prey on *S. variabilis* (personal observations). *Haematopus ater* was observed at Algarrobo and Los Molles 2, but not at other sites. Effects of predation on *S. variabilis* by this species are likely to be inseparable from the effects of *Cinclodes*.

In areas where *Cinclodes* spp. are present, differences in morph ratios between accessible and inaccessible habitats provide clear evidence for the selection of non-cryptic morphs by *Cinclodes*. At high *Cinclodes* densities, the bias towards mimetic morphs in the limpet population is more pronounced (Table 1, Figure 3). Shorebirds, even though they occur at much higher densities than *Cinclodes* in some areas, have a negligible impact on *Scurria* morph ratios as evidenced by insignificant differences in morph ratios between accessible and inaccessible microhabitats (Table 1). This may be due to the concentration of their feeding activity in the low- rather than mid-shore region (personal observations). Some wader species may not prey on *Scurria* at all, and the nocturnal feeding habits of some species (movement rather than coloration of the prey probably being the prime visual cue to predators at night) would not result in morph-specific predation.

The impact exerted by visual, selective predators, chiefly

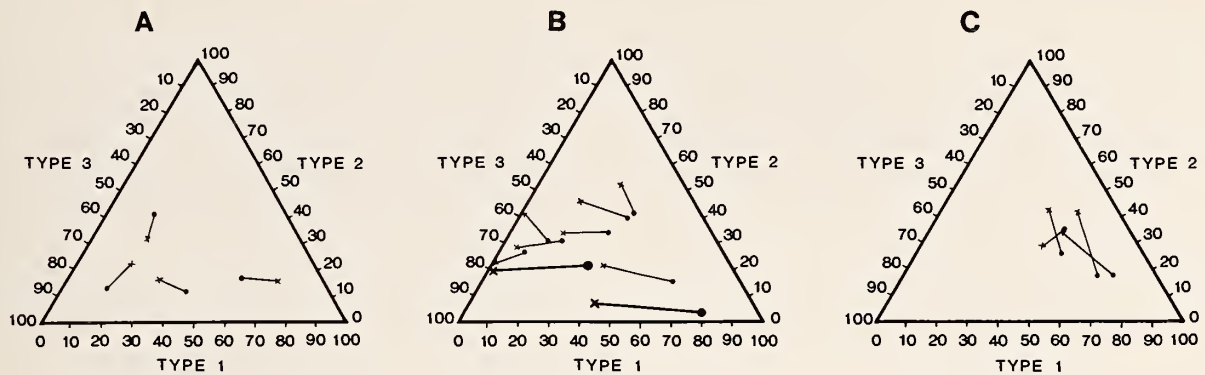


Figure 3

Ternary diagrams illustrating the relationship between morph ratios of *Scurria* and predation. A, no avian predators; B, with *Cinclodes*; C, with waders. Lines join crosses (accessible microhabitats) to solid circles (inaccessible microhabitats) at the same site. The larger crosses and dots in Figure 3B refer to sites at which the density of *Cinclodes* was >1 bird per 100 m of shore.

Cinclodes, on the survival of different morphs of *Collisella* is striking, but localized to the extent that morph ratios on inaccessible slopes within *Cinclodes* territories and in wader feeding areas do not differ from one another or from the morph ratios in areas where there are neither *Cinclodes* nor waders present. These observations suggest that, although *Cinclodes* may have a local influence on the occurrence of phenotypes, these birds are not exerting a detectable local genetic influence on the population, nor is limpet density correlated with predator abundance (Table 1). The presumed pelagic larval stage of *Scurria* limpets would tend to confound anything other than major local genetic influences. A situation exists on the central Chilean coast in which the predator apparently exerting the major influence on *Scurria* phenotypes in central Chile occurs patchily and at low density and appears to have no influence on *Scurria* density. At the same time, *S. variabilis* shows an effective and highly elaborate polymorphism that has arisen in the apparent absence of any strong selective force that is still evident today. However, despite the fact that predatory pressure is low, the selectivity of the predator provides the mechanism for the maintenance of polymorphism in the prey, inasmuch as the incipient mimic (*sensu* BROWER *et al.*, 1971), the Type 2 *Scurria*, enjoys a selective advantage over the non-cryptic Type 1 individuals. The absolute abundance of Type 1 morphs suggests that, under present predation pressures, polymorphism is not essential for the survival of the *S. variabilis* population as a whole but strongly favors the survival of cryptically mimetic individuals in the presence of predatory *Cinclodes*.

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